

The University of Chicago

HISTOLOGICAL COMPARISON
OF CUCUMBER FRUITS DEVELOPING
PARTHENOCARPICALLY AND
FOLLOWING POLLINATION

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1941

By

JOSEPH ORAN YOUNG

Reprinted from
THE BOTANICAL GAZETTE
Vol. 105, No. 2, September, 1943

The University of Chicago

HISTOLOGICAL COMPARISON
OF CUCUMBER FRUITS DEVELOPING
PARTHENOCARPICALLY AND
FOLLOWING POLLINATION

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1941

By
JOSEPH ORAN YOUNG

Reprinted from
THE BOTANICAL GAZETTE
Vol. 105, No. 2, September, 1943



HISTOLOGICAL COMPARISON OF CUCUMBER FRUITS DEVELOPING PARTHENO-CARPICALLY AND FOLLOWING POLLINATION

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 554

J. O. YOUNG

Introduction

Parthenocarpy in the cucumber has long been recognized by horticulturists, but it was first made the subject of botanical investigation in 1902 by NOLL (15), who defined the term and observed fruits containing abortive seeds with undersized seed coats. Two years later KIRSCHNER (13) reported a doubtful case in which 78 out of 95 seeds produced in a single unpollinated cucumber were viable. HARTLEY (12) reported the stimulation of fruit development in tobacco by treating the stigmas with *Azalea* pollen, corn flour, magnesium sulphate, or air-slaked lime. FITTING (4), YASUDA (20), and GUSTAFSON (10) have achieved similar results with pollen extracts.

Since the development of the growth-substance concept, several investigators, notably GUSTAFSON (8, 9), GARDNER and MARTH (6), and WONG (19), have succeeded in inducing fruit development by growth-promoting chemicals. These investigators worked chiefly with species of the Cucurbitaceae and Solanaceae, as well as with holly and strawberry. GARDNER and KRAUS (5) made a histological study of artificial parthenocarpy in the holly, noting that development closely parallels that of pollinated fruits, except for the disintegration of the megagametophyte and the absence of embryo and endosperm. VAN OVERBEEK *et al.* (18) reported the formation of pseudo-embryos in *Datura* fruits which had been injected with auxin.

TUKEY (17) showed that living em-

bryos are essential for development of cherry and peach fruits. He correlated his findings with the three stages in the growth curves of these drupe fruits. Using the *Avena* test method, GUSTAFSON (7, 11) reported that auxin concentration of fruits is highest in developing ovules and associated tissues, and that it is higher in normally seeded than in parthenocarpic fruits of the same species. He concluded that auxins play a major role in fruit development.

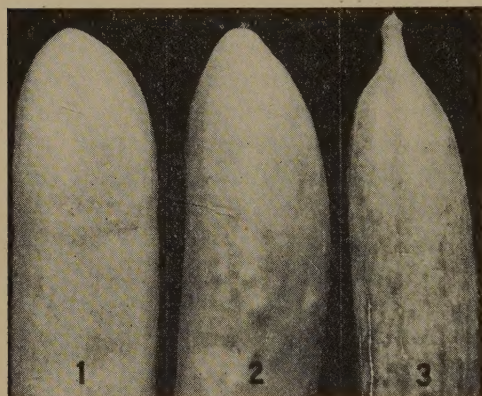
Certain varieties of cucumber regularly produce fruits without pollination. The results obtained with the variety Rollison's Telegraph, which exhibits natural parthenocarpy, are given here.

METHODS.—Seeds were planted February, 1941, in rich garden soil and grown on a well-lighted greenhouse bench. The plants were kept watered at all times but no attempt was made precisely to control the temperature or the humidity. During the later stages of the experiment the plants were supplied with complete nutrient solution high in nitrate to insure continued vigorous growth. The vines were trained upon a horizontal trellis about 7 feet above the floor level, and the developing fruits were allowed to hang without support.

Uniform pistillate flowers were selected at two developmental stages and treated with 2 per cent indoleacetic acid in lanolin paste. Controls were treated with pure lanolin. One lot was treated at full bloom and a second lot at approximately 4 days before full bloom. At the

time of anthesis the ovaries used ranged from 3.5 to 4.5 cm. in length. Larger or smaller ovaries were discarded. Four days before full bloom the developing ovaries were 1.8–2 cm. long and the still-green petal lobes extended about 4 mm. beyond the calyx.

The upper portion of the perianth, including the stigma and staminodia, was removed by a transverse cut through the



FIGS. 1-3.—Apical portions of fully developed fruits: Fig. 1, pollinated; untreated fruits and controls treated at full bloom were similar in appearance. Fig. 2, treated with indoleacetic acid at full bloom; fruits treated with pure lanolin 4 days before full bloom were similar in appearance. Fig. 3, treated with indoleacetic acid 4 days before full bloom, showing apical tumor.

nectary, and the indoleacetic acid in lanolin paste was spread in a thin layer over the freshly exposed surface. The lower part of the floral tube remained attached to the ovary by the narrow neck about 1 mm. long. Pure lanolin was used for controls. A third lot of flowers was hand-pollinated, and a fourth was allowed to develop without treatment.

Portions of the fruits were fixed in Navashin's fluid and transferred to paraffin by the tertiary butyl-alcohol method. The material was transferred from the fixing fluid directly to a mixture containing ethyl alcohol 50 per cent, ter-

tiary butyl-alcohol 20 per cent, and water 30 per cent. This procedure gave as good results as the more laborious method of washing in water and running through a longer series of changes. Sections were cut at 10 μ and stained in safranin, gentian violet, and orange G.

Gross development

Virtually all the ovaries, including those untreated, developed rapidly for several days. Toward the end of the experiment, however, the presence of large developing fruits inhibited early growth of other fruits on the same vine. Fruits treated with the acid 4 days before full bloom were decidedly smaller than any of the others.

POLLINATED FRUITS.—Within a day or two after pollination the perianth and included structures began to wither, and usually they were completely dried within a week. These dead tissues usually fell away and left a smooth rounded scar (fig. 1). At the end of 20 days many of the ovules had attained a length of 12 mm. and the hardened seed coats inclosed well-formed embryos (fig. 4).

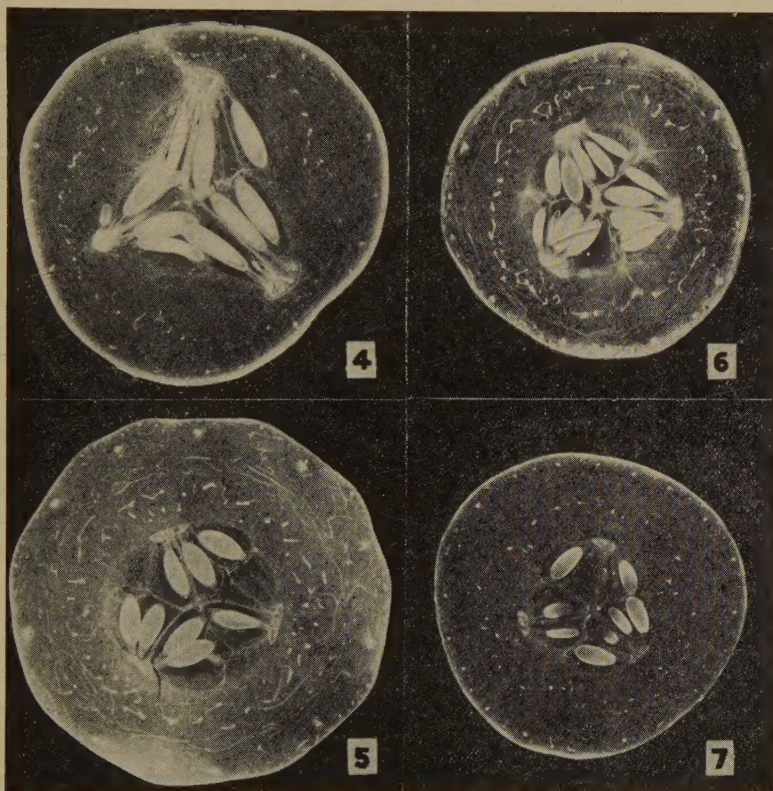
UNTREATED FRUITS.—In external appearance the untreated fruits developed identically with the pollinated fruits. Some of the ovules attained full size, but more frequently they were slightly smaller (fig. 5) and the seed coats were often sunken on the flattened sides. In no cases were embryos found.

FRUITS TREATED AT FULL BLOOM.—Fruits treated with indoleacetic acid at full bloom differed from the untreated controls in that the apical tissues below the cut surface remained alive until harvested and sometimes increased slightly in size, resulting in a small protuberance at the tip of the mature fruit (fig. 2). The ovules were slightly smaller than those of the untreated fruits (fig. 6). In corre-

sponding controls treated with pure lanolin the neck and perianth tissues dried out in the same manner as those on pollinated or untreated plants.

FRUITS TREATED 4 DAYS BEFORE FULL BLOOM.—Fruits treated with indoleacetic

acids of the floral tube and neck became lighter in color and a slight swelling was observed. After 4–5 days the tumors began to develop a bright green color throughout. Subsequent growth of the tumors was more rapid, and maximum



FIGS. 4–7.—Cleared cross sections of fully developed fruits: fig. 4, pollinated, showing embryos; fig. 5, untreated; fig. 6, treated with indoleacetic acid at full bloom; fig. 7, treated with indoleacetic acid 4 days before full bloom.

acid 4 days before full bloom developed characteristic apical tumors, involving the tissues of the nectary, floral tube, and the neck. The tumors reached a maximum diameter of slightly more than 1 cm. and a length of nearly 2 cm. (fig. 3). At the time of treatment the nectary tissue was light yellow and the lower part of the floral tube only slightly green. During the first 2 days after treatment the tis-

size was usually attained in 10–15 days. The tissues of the nectary proliferated more extensively than those of the floral tube and greatly overtopped the latter structure. In no case did the tumors develop the large irregular masses reported for stems and fruits of the bean (14). No root primordia were observed. Ovules attained a final size decidedly smaller than those of the controls (fig. 7). Hardening

of the integuments was markedly inhibited and restricted to the micropylar end of the ovule.

The apical portions of controls treated with pure lanolin at 4 days prior to full bloom remained intact for several days. At the end of 24 days, tissues of the floral tube, nectary, and part of the neck were dead but no periderm or scar tissue had formed. At this time the gross appearance was similar to that of fruits treated with indoleacetic acid at full bloom (fig. 2), except that there was more dead apical tissue.

Histological details

FERTILIZED OVULES.—No comprehensive published account of ovule development in the cucumber has been found. TILLMAN (16) investigated the megagametophyte development and embryology. She noted the massive nucellus, the swelling of the pollen tube, digestion of cells within the nucellar beak, and the attainment by the ovules of a strictly anatropous position. The findings of the writer are similar in all major respects. FICKEL (3) showed that the major portion of the seed coat is derived from the outer integument, the inner integument attaining a thickness of only two cell layers. BARBER (1) added a few details of cell size and arrangement but erroneously figured an inner integument several cells in thickness early in development.

Four days before full bloom the megaspore mother cell may be clearly distinguished two to four cell layers from the tip of the nucellus. Continued tangential division of the overlying cells results in the development of a long nucellar beak, which is discernible at the time of anthesis. The inner integument develops as a covering two or three cells in thickness, which finally closes over the nucellar beak. The outer integument

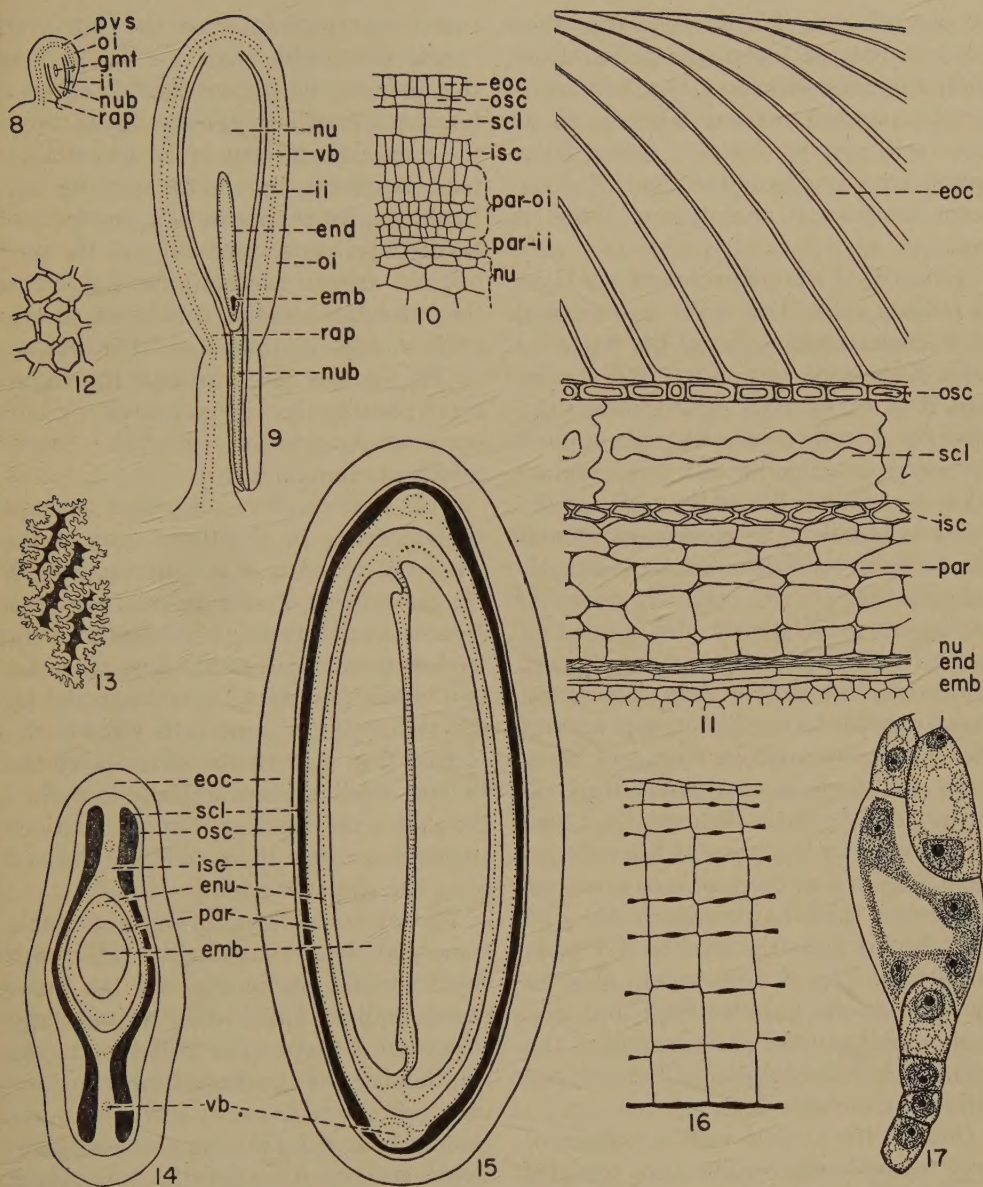
arises as a more massive layer and may be eight cells in thickness by the time of full bloom. A vascular strand extends through the raphe to the chalaza and is continuous with a strand which extends through the outer integument as far as the base of the nucellar beak (fig. 8).

At full bloom meiosis has been completed and the gametophyte is partially or fully developed. It occupies a position just proximal to the base of the nucellar beak. At this stage mitotic activity is evident in the integuments and at the chalazal end of the nucellus.

Fertilization is accomplished in ovules near the apical end of the ovary within 72 hours after pollination. Just before fertilization the pollen tube enlarges in the proximal portion of the nucellar beak and nucellar cells in this region are digested. Soon after fertilization, cells of the nucellus adjacent to the embryo sac become meristematic, and several mitotic divisions occur. Eight days after full bloom the embryo is a small, slightly elongated cellular mass (fig. 9). At this stage mitotic activity is still in progress but all tissues of the seed coat are clearly defined.

Subsequent development of the seed coat involves differentiation and maturation of the several tissues. Comparison of figure 10 (8 days from full bloom) and figure 11 (20 days after full bloom) brings out the development of tissue types in the seed coat.

The seed coat may be compared to a rigid laminated sac of many layers. In the mature seed, cells of the innermost layer are parenchymatous. This tissue is of mixed origin. The inner portion derives from the inner integument and the remainder arises from the inner four or five tiers of cells of the outer integument. As the seed coat matures the exterior tissues increase in size more than the interi-



FIGS. 8-17.—Fig. 8, longitudinal section of ovule at full bloom; $\times 35$. Fig. 9, same, 8 days after full bloom; $\times 35$. Fig. 10, portion of longitudinal section through seed coat 8 days after full bloom; $\times 350$. Fig. 11, same, 24 days after full bloom; $\times 350$. Fig. 12, stellate cells from tissue surrounding vascular bundle; $\times 450$. Fig. 13, elongated stone cells from macerated seed coat; $\times 200$. Fig. 14, cross section of mature seed near hilum; $\times 35$. Fig. 15, same, through center of seed; $\times 35$. Fig. 16, cells of outermost layer of seed coat as seen in cross section through seed, showing thickenings on cell walls; $\times 350$. Fig. 17, anomalous development of megagametophyte: four cells at lower part of figure are at micropylar end; $\times 750$ (emb, embryo; end, endosperm; enu, endosperm and nucellus; eoc, elongated outer cells; gmt, megagametophyte; ii, inner integument; isc, inner layer of thick-walled derivatives of stellate cells; nu, nucellus; nub, nucellar beak; oi, outer integument; osc, outer layer of thick-walled derivatives of stellate cells; par, parenchyma; pvs, provascular strand; rap, raphe; scl, elongated stone cells; vb, vascular bundle).

or parenchyma. The interior cells thus become flattened and are pulled from their original positions, so that at maturity the parenchymatous layer is about five cells in thickness. Intercellular spaces are formed and the identity of the inner integument as a distinct tissue is lost.

External to the parenchyma is a layer of stellate cells. This layer is composed of a single tier of cells on the flattened sides of the seed, but on the lateral margins it is many cells in thickness. The vascular bundle which extends around the seed is imbedded within this marginal layer of stellate cells. In the region of the vascular bundle little growth occurs and the stellate condition becomes best developed (fig. 12). At maturity each cell has many projections which extend in various directions and abut on adjacent projections from other cells. The tissue thus formed is lattice-like in appearance, the large intercellular spaces being merged to form a continuous three-dimensional labyrinth. Where this tissue is only one tier in thickness the cells become flattened as the seed coats enlarge. Thickening and hardening of the cell walls begins after the twelfth day from full bloom. This is first evident close to the base of the nucellar beak and proceeds rapidly to the chalazal end of the seed. No sclerenchyma is developed within the nucellar beak.

Outside the stellate cells is a layer of large stone cells which are greatly elongated in the longitudinal plane of the seed axis. Examination of macerated tissue shows these cells to be roughly rectangular in surface view, but the margins are deeply and irregularly incised (fig. 13). The lumen of each cell is narrow and branched and thus appears to be discontinuous when the seed is cut in median longitudinal section. In a few cells, how-

ever, the continuity of the lumen is clearly discernible (fig. 11). The cells of this tier are tightly dovetailed together, forming a hard impermeable layer. Near the nucellar beak this layer does not extend completely around the seed (fig. 14). In this region the tissue is in the form of two bands over the flat sides of the seed but not around the margins. Lateral to the vascular bundles this layer is two to four cells in thickness. The discontinuity of this layer around the hypocotyl permits the emergence of the embryo at germination when the empty seed coats remain intact.

The next layer is another tier of stellate cells. In the distal end of the seed coat this tissue is continuous with the inner layer of stellate cells (fig. 14). A cross section through the center of the seed, however, shows that here there are two layers of stellate cells separated by the tier of large stone cells already described (fig. 15). In the outer layer the stellate condition is practically lost when the cell walls thicken, but the various stages show that these cells are derived from the stellate type.

The outermost layer of the seed coat is composed of very elongate cells with characteristic thickenings on the inner radial walls. These cells are radially elongated 8 days after full bloom. As lengthening and maturation continue they become appressed, with the outer ends lying in the direction of the chalaza. Cross sections through the seed show that these cells develop in an orderly spatial arrangement. Since these cells overlap for most of their length, it appears in cross-sectional view that there are several distinct layers (fig. 16).

The elongated cells of this outer layer are continuous over the beak but lack thickenings in this region. The remainder of the beak is composed of a few stellate

cells and parenchyma. A constriction occurs at the base of the beak, and when the seed is broken away a considerable portion of the raphe, integuments, and nucellar remnants is lost (fig. 9).

In the mature seed the nucellus has been reduced to a membrane of collapsed cell walls, and a single layer is all that remains of the endosperm.

UNFERTILIZED OVULES.—Many stages in meiosis and megagametophyte development were carefully observed, but no deviations from the normal were found subsequent to treatment with indoleacetic acid, even when the application was made before the onset of the meiotic process. Three days after full bloom, however, the absence of the pollen tubes in ovules of unpollinated fruits was noted and the cells of the nucellar beak were not digested. No renewal of meristematic activity in nucellar cells adjacent to the megagametophyte occurred, as is the case when young embryos are present. In other portions of the ovule, divisions continued until 8 days after full bloom, or about as long as they do following fertilization.

The megagametophytes of the parthenocarpic fruits were occasionally observed to enlarge considerably. This sometimes continued for as long as 8 days after full bloom, but more often degeneration began about the fifth day. The fusion nucleus and the egg were usually the last recognizable remnants of the megagametophyte. These were sometimes discernible 16 days after full bloom. Even in the absence of an embryo, the nucellus developed into a massive tissue which completely filled the integuments. The cavity left by the degenerating gametophyte was often extended by cellular disintegration in the center of the nucellus.

Proliferation of gametophytic cells

was observed in a single case. In a section of an ovule fixed 8 days after prebloom treatment with indoleacetic acid the condition shown in figure 17 was clearly seen. The free nuclear tissue is suggestive of endosperm and apparently has arisen by divisions of the fusion nucleus. The four cells at the micropylar end of the figure may have been derived from the egg. Since the antipodals have been observed to degenerate early in this variety, it would seem most probable that the two large cells at the chalazal end are of nucellar origin.

In the ovules of all fruits treated with indoleacetic acid and in the controls cell division continued long enough so that the pattern of the mature seed coats was definitely established. When the acid was applied 4 days before full bloom, hardening of the seed coats was greatly reduced and usually did not extend more than halfway to the chalazal end of the seed. When treatments were made at full bloom, hardening proceeded somewhat further, while in the controls the integuments sometimes reached a stage of development nearly equal to that of ovules containing embryos.

The preceding description is based on the most completely developed ovules, which usually are found near the apical end of the fruit. As a rule the ovules near the stem end are progressively smaller, and many of them never exceed 1–2 mm. in length.

APICAL TISSUES.—Following pollination, the stylar canal tissue is digested or disrupted within 48 hours by the developing pollen tubes. The adjacent intact cells become elongated in a radial direction, but meristematic activity is not initiated in any part of the floral tube, nectary, stylar tissue, or neck. There was some increase in the thickness of cell walls in the peripheral parenchym-

atous cells of the neck at 4 days after full bloom. By this time the nectary tissue has degenerated and a periderm may have begun to form at the base of the neck. At 8 days after full bloom the periderm is well formed, and on its outer surface cell walls are appreciably thickened. All the distal dried-out tissues may now fall away, or they may remain attached. At 20 days after full bloom pitted stone cells were found abundantly in the tissue immediately beneath the apical periderm. Apical tissues of untreated plants and of the controls treated with lanolin at full bloom dried out in much the same manner, except that the changes incident to penetration of the pollen tubes did not occur and a periderm developed across the tissue of the styler canal.

Following treatment with indoleacetic acid at full bloom, disintegration of the apical tissues was greatly retarded. At the end of 20 days the tissues of the nectary and floral tube were usually shriveled, but cells of the neck were alive. A periderm was not generally formed at the base of the neck, but tangential cell divisions were commonly observed in the peripheral neck region. Cell walls in this zone often became somewhat thickened, with conspicuous pits, but no stone cells or fibers were found. There was evidence of slight proliferation throughout the parenchymatous cells of the neck.

Earlier than 4 days before full bloom meristematic activity was abundant in the tissues of the neck. New cell walls were formed, chiefly in the transverse plane of the axis, so that the cells of the parenchyma presented a more or less tabular or ladder-like appearance. In lanolin controls 4 days before full bloom this pattern was recognizable as long as 24 days later. Except for moderate increase in cell size, the tissues of the neck remained much as they were at the time

of treatment. The cells of the nectary and floral tube gradually degenerated. Only slight thickening of cell walls was observed, and no sclerotic or vascular tissues were differentiated subsequent to pre-bloom treatments with pure lanolin paste.

When the 2 per cent acid-lanolin mixture was applied 4 days before full bloom, there was a prompt response in the floral tube, nectary, and neck. Cells immediately below the cut surface of the nectary were slightly enlarged after 24 hours; the nuclei were larger and showed greater affinity for the stains; the cytoplasm increased in amount and was often extended across the large central vacuoles. Apparently normal cell divisions occurred. Continued increase in cell size was chiefly in the direction of the fruit axis, so that markedly elongate cells were formed. By repeated mitotic divisions these cells were divided into groups of smaller cells. The outlines of the parent cell walls were often discernible for several days, much as described in stems of *Lilium* by BEAL (2). In the nectary of the cucumber, however, the new walls were all formed in a single plane, so that in longitudinal section the entire unit of derived cells appeared as a single row. After the initial activity, mitotic divisions gradually decreased and stopped. Cell enlargement continued for about 12 days, at which time the tumors had reached their maximum size. Responses in the floral tube were much less striking than those of the nectary, and there was no evidence of meristematic activity in the styler canal tissue. Divisions in other than the transverse plane were observed in the neck, particularly in the outer ring of bundles and adjacent parenchyma. Within the bundles cambial activity was initiated and a few parenchymatous derivatives

were formed. In no case were root primordia formed, and no new bundles were differentiated in the proliferated tissue. Meristematic activity ceased after a relatively short period. Thereafter all cells except mature conducting elements of the xylem increased in size, and density of protoplasmic contents decreased throughout. In old tumors the walls of eight or ten peripheral cell layers in the neck region increased considerably in thickness and showed conspicuous pits. Conducting elements of the phloem were no longer recognizable as such, and a few very thick-walled pitted fibers were sometimes found in the outer part of the external phloem.

When the transverse cut was made in such a way that only a portion of the nectary was removed, there was very little activity beneath the uninjured surface; when the cut was above the nectary, proliferation was marked only in the styler tissues. In this case the style became considerably elongated.

Discussion

Although relatively few species have been investigated, wide variation has been found in the extent of seed-coat development in artificially produced parthenocarpic fruits. In the present investigation there was a progressive decrease from the normal seed-coat size in response to different treatments in the following order: after pollination, the seeds were large; untreated fruits and controls treated with pure lanolin produced slightly smaller abortive seeds; following indoleacetic acid at full bloom development was still further retarded; and the acid applied 4 days before full bloom resulted in the smallest seeds (approximately half the usual size). The small seed coats were only partially hardened. Fruits of the last-mentioned series were

decidedly smaller than those which were pollinated. Untreated fruits and controls treated with pure lanolin were as large as those which were pollinated. In the cucumber variety studied, therefore, the presence or absence of an embryo is not a major factor affecting the size of the fruit. Whether the indoleacetic acid has a direct retarding effect on fruit development or acts through changes in the food supply or in some other manner is not known. Chemical analyses of fruits produced by artificial parthenocarp are needed. Further histological studies to show the relative importance of cell division and cell enlargement to final fruit size would also be desirable.

Following pollination, the nectary, floral tube, and neck of the flower rapidly dry out. The development of an active growing tissue in response to early application of the acid-lanolin mixture from a portion of the flower that would soon shrivel and die in the usual course of events is of interest. Since no true abscission layer is formed at the base of the cucumber neck, this is of different character from the effects of growth substances on abscission of petioles and other organs. In contrast to the results in the bean, the proliferation of tissues of the cucumber fruit is limited to a fairly short period of time, and no vascular derivatives or root primordia are formed.

Summary

1. The development of cucumber fruits of a naturally parthenocarpic variety (Rollison's Telegraph) was studied before and following pollination. The development of megagametophyte, embryo, and seed coats was observed in detail. Tissues of the perianth, stigma, nectary, and neck shriveled within a week after pollination, and a protective periderm formed at the apex of the live tissue

beneath. Twenty days after full bloom hardened seed coats contained large well-developed embryos.

2. Development of untreated fruits in which there was no pollination was essentially the same, except for the absence of embryos and endosperm, the disintegration of megagametophytes, and the slightly smaller size of the seed coats.

3. In other cases transverse cuts were made through the lower portion of the floral tube and a 2 per cent mixture of indoleacetic acid in lanolin was applied to the cut surface.

4. When application of the mixture was made 4 days before full bloom, apical tumors were formed, involving tissues of the nectary, floral tube, and neck. These reached maximum size in about 12 days. Neither vascular tissues nor root primordia were differentiated in the tissues of the tumors. Ovules developed to about half normal size, and seed coats became partially hardened.

5. When pure lanolin was applied 4 days before full bloom, death of the apical tissue was greatly retarded and usually no periderm was formed. Ovules developed as in untreated controls.

6. When indoleacetic acid in lanolin was applied at full bloom the apical tissues remained alive but proliferated very little. Ovules were intermediate in size between those of controls and those of fruits given the pre-bloom treatments with indoleacetic acid in lanolin.

7. When pure lanolin was applied at full bloom, development was essentially the same as that of untreated controls.

8. In the unfertilized ovules of parthenocarpic fruits the nucellus generally developed into a massive tissue with a large central cavity.

9. Meiosis and megagametophyte development were not noticeably affected by any of the treatments.

10. In a single instance following premeiotic treatment with indoleacetic acid there was some proliferation of gametophytic tissue.

The writer expresses his appreciation to Dr. J. M. BEAL for his interest and aid in this work. Valuable suggestions were also made by other members of the department of botany.

DEPARTMENT OF BOTANY
UNIVERSITY OF CHICAGO

LITERATURE CITED

1. BARBER, KATE G., Comparative histology of fruits and seeds of certain species of Cucurbitaceae. *BOT. GAZ.* 47:263-310. 1909.
2. BEAL, J. M., Histological responses of three species of *Lilium* to indoleacetic acid. *BOT. GAZ.* 99:881-911. 1938.
3. FICKEL, J. F., Ueber die anatomie und Entwicklungsgeschichte der Samenschalen einiger Cucurbitaceen. *Bot. Zeit.* 34:737-744; 753-760; 769-776; 785-792. 1876.
4. FITTING, H., Weitere entwicklungsphysiologische Untersuchungen an Orchideenblüten. *Zeitschr. Bot.* 2:225-267. 1910.
5. GARDNER, F. E., and KRAUS, E. J., Histological comparison of fruits developing parthenocarpically and following pollination. *BOT. GAZ.* 99:355-376. 1937.
6. GARDNER, F. E., and MARTH, P. C., Parthenocarpic fruits induced by spraying with growth promoting compounds. *BOT. GAZ.* 99:184-195. 1937.
7. GUSTAFSON, F. G., Auxin distribution in fruits and its significance in fruit development. *Amer. Jour. Bot.* 26:189-194. 1939.
8. ———, Induced parthenocarpy. *BOT. GAZ.* 99:840-844. 1938.
9. ———, Induction of fruit development by growth promoting chemicals. *Proc. Nat. Acad. Sci.* 22:628-636. 1936.
10. ———, Parthenocarpy induced by pollen extracts. *Amer. Jour. Bot.* 24:102-107. 1937.
11. ———, The cause of natural parthenocarpy. *Amer. Jour. Bot.* 26:135-138. 1939.

12. HARTLEY, C. P., Injurious effect of premature pollination, with general notes on artificial pollination and the setting of fruits without pollination. U.S. Bur. Plant Ind. Bull. 22. 1902.
13. KIRSCHNER, O., Parthenogenesis bei blütenpflanzen. Ber. deutsch. Bot. Ges. 22:83-97. 1904.
14. KRAUS, E. J., BROWN, NELLIE A., and HAMNER, K. C., Histological reactions of bean plants to indoleacetic acid. BOT. GAZ. 98:370-420. 1936.
15. NOLL, F., Über Fruchtbildung ohne vorausgegangene Bestäubung (Parthenokarpie) bei der Gurke. Sitz Ber. der Niederhein. Gesell. Natur. Heilkunde. Bonn. 1902.
16. TILLMAN, OPAL L., The embryo sac and embryo of *Cucumis sativus*. Ohio Naturalist 6:423-430. 1906.
17. TUKEY, H. B., Development of cherry and peach fruits as affected by destruction of the embryo. BOT. GAZ. 98:1-24. 1936.
18. VAN OVERBEEK, J., CONKLIN, M. E., and BLAKESLEE, A. F., Induction of pseudo-embryos in *Datura* by auxin treatment. Abstract, Amer. Jour. Bot. 27:188. 1940.
19. WONG, C. Y., A study of chemically induced parthenocarpy in certain horticultural plants, with special reference to the watermelon. BOT. GAZ. 103:64-86. 1941.
20. YASUDA, S., Parthenocarpy caused by the stimulation of pollination in some plants of the Cucurbitaceae. Agr. and Hort. 10:1385-1390. 1935.

